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Recovery potential modelling of Mountain Sucker (*Catostomus platyrhynchus*), Milk River populations

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Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the Milk River populations of Mountain Sucker (*Catostomus platyrhynchus*) as Threatened in Canada (COSEWIC 2010). Here we present population modelling to assess allowable harm, determine population-based recovery targets, and conduct long-term projections of population recovery in support of a recovery potential assessment (RPA). Our analyses demonstrated that the dynamics of Mountain Sucker populations are very sensitive to perturbations that affect the survival of immature individuals (from hatch to age 2), and to the collective survival of adults (ages 2-6). Harm to these portions of the life cycle should be minimized to avoid jeopardizing the survival and future recovery of Canada's Milk River populations. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), we propose a population abundance recovery target of 6400 adult Mountain Sucker, requiring 3.0 – 16.6 ha of suitable habitat. Current estimates of mean vital rates suggest the population may be in decline, although parameter values are sufficiently uncertain that this may not be the case. Recovery strategies which incorporate improvements in the most sensitive vital rates of Mountain Sucker are most likely to improve the population growth rate; improvements of 20% in survival of all life stages significantly delayed extinction risks, and improvements of 84% and 28% respectively to juvenile and adult survival stimulated population growth.

Modélisation du potentiel de rétablissement des populations de meunier des montagnes (*Catostomus platyrhynchus*) de la rivière Milk

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a désigné les populations de meuniers des montagnes (*Catostomus platyrhynchus*) de la rivière Milk comme étant menacées au Canada (COSEPAC 2010). Ce document présente la modélisation de la population afin d'évaluer les dommages admissibles, d'établir les objectifs de rétablissement en fonction de la population et d'effectuer des projections à long terme du rétablissement de la population en vue d'appuyer l'évaluation du potentiel de rétablissement (EPR). Nos analyses prouvent que la dynamique des populations de meunier des montagnes est très sensible aux perturbations qui affectent la survie des individus immatures (de l'éclosion à l'âge 2) et la survie collective des adultes (âges 2 à 6). On doit réduire au minimum les dommages ravages sur ces étapes du cycle de vie afin d'éviter de mettre en péril la survie et le rétablissement futur des populations de la rivière Milk au Canada. En nous basant sur un objectif de durabilité démographique (c.-à-d. une population autonome à long terme), nous proposons une cible de rétablissement de l'abondance de 6 400 meuniers adultes, nécessitant entre 3 et 16,6 ha d'habitat propice. Les estimations actuelles des indices vitaux moyens semblent indiquer un déclin de population, mais l'incertitude qui pèse sur les valeurs des paramètres indiquent que ce n'est pas nécessairement le cas. Les stratégies de rétablissement qui prévoient des améliorations des indices vitaux de meunier des montagnes les plus sensibles provoqueront une augmentation presque certaine des taux de croissance des populations; des améliorations du taux de survie de 20 % pour tous les stades biologiques ont permis de retarder considérablement le risque d'extinction; en améliorant le taux de survie des juvéniles et des adultes de 84 % et 28 % respectivement, on a stimulé la croissance de la population.

INTRODUCTION

The Milk River designatable unit (DU2) of Mountain Sucker *(Catostomus platyrhynchus*) was assessed in November 2010 as *Threatened* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). DU2 consists of three isolated populations (no mixing of individuals) in Alberta (Milk rivers population) and Saskatchewan (Battle Creek population and Frenchman River population). In accordance with the *Species at Risk Act* (SARA), which mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation in Canada, Fisheries and Oceans Canada has developed the recovery potential assessment (RPA; DFO 2007) as a means of providing information and scientific advice. There are three components to each RPA: an assessment of species status, the scope for recovery, and scenarios for mitigation and alternatives to activities (DFO 2007). This last component requires the identification of recovery targets and timeframes for recovery, and measures of uncertainty associated with the outcomes of recovery efforts. Here, we contribute to components two and three by assessing allowable harm, identifying recovery targets, projecting recovery timeframes and identifying mitigation strategies for Canadian populations of Mountain Sucker. This work is based on a demographic approach developed by Vélez-Espino and Koops (2007; 2009a; 2009b), which uses a population-based recovery target, and provides long-term projections of population recovery under a variety of feasible recovery strategies.

METHODS

Our analysis consisted of four parts: (i) information on vital rates was compiled and used to build projection matrices, using uncertainty in life history to represent variation in the life cycle for stochastic simulations; (ii) we used these matrices in a stochastic perturbation to determine the sensitivity of the population growth rate to changes in each vital rate, as well as to determine allowable harm following Vélez-Espino and Koops (2007, 2009a, 2009b); (iii) the projection matrices were used to simulate risk of extinction, and to estimate the minimum viable population (MVP); and (iv) using the MVP as a recovery target, we simulated the effects of potential recovery efforts on a typical population.

SOURCES

Where possible, life history estimates for Mountain Sucker were based on sampling data from Canadian populations collected between 2003 and 2009, with the bulk of these samples (75%) collected in 2006 from Lee Creek, St. Mary River, and Milk River (D. Watkinson, DFO unpubl. data). Where possible, estimates were supplemented from the literature.

MATRIX MODEL

Using a matrix approach, the life cycle of Mountain Sucker was represented with annual projection intervals and by a post-breeding age-structured projection matrix (Caswell 2001; Figure 1). Individuals were assumed to first mature at age 2 or 3, and reach a maximum age of 6 years (see following section). The model therefore represents seven age classes: young of the year (age 0), juveniles (age 1) and 5 adult classes.

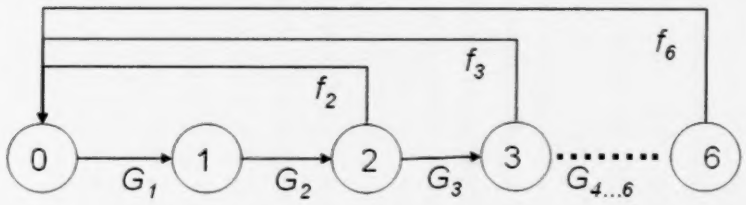
Elements of the age-structured matrix included the fecundity coefficient of age class j (F_j), and the age-specific annual survival probability from age j-1 to age j (G_j). Fecundity coefficients (F_j) represent the contribution of an adult in age class j to the next census of age-0 individuals. Since a post-breeding model is assumed, the coefficient F_j includes the annual survival

probability of adults from age *j*-1 to age *j*, as well as the age-specific fertility upon reaching age *j* (f_j) such that

$$F_j = G_j f_j$$

where f_j is the product of a stage's average number of eggs (m_j), the proportion of females (assumed to be 50%), and the inverse of the average spawning periodicity (assumed to be 1).

a)



b)

$$M = \begin{pmatrix} 0 & F_2 & F_3 & \ldots\ldots & F_6 & 0 \\ G_1 & 0 & \ldots\ldots & & & \\ 0 & G_2 & 0 & & & \\ & 0 & G_3 & \ldots & & \\ & & \ldots & \ldots & 0 & \\ 0 & \ldots & & 0 & G_6 & 0 \end{pmatrix}$$

c)

$$\begin{pmatrix} 0 & 27 & 172 & 317 & 470 & 619 & 0 \\ 0.0036 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.18 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.33 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.42 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.48 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.52 & 0 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding the age-structured projection matrix (b), and mean values of matrix elements (c) used to model the population dynamics of Mountain Sucker. F_j represents fecundities, and G_j the survival probabilities from age j-1 to age j. Note that fertility is positive for the age 1 class (F_2) since some individuals recorded as age 1 in census t will mature upon their second birthday (if they survive) and produce offspring that will be counted at census t+1 (Caswell 2001).

Parameter Estimates

To estimate parameters for the matrix model (summarized in Table 1) we first established a mean size for each age class. This was accomplished by fitting a von Bertalanffy growth curve to mean total lengths-at-age (weighted by sample size) of Mountain Sucker from Flathead Creek, Montana (Hauser 1969). The growth curve relates size and age using the formula: $L_t = L_\infty (1 - e^{-k(t-t_0)})$, where L_t is size at time t, t_0 is the hypothetical age at which the fish would have had length 0, L_∞ is the asymptotic size, and k is a growth parameter. Because the curve was fitted to means instead of raw data, L_∞ was unrealistically overestimated and k was underestimated. When the curve was forced to pass through a hatch size of 5mm, the

resulting predicted sizes matched well with Canadian size frequencies (Figure 2). Note that Hauser (1969) reported average sizes based on the last otolith (i.e., overwinter size), whereas the Canadian length frequency was collected during the summer and fall. Therefore, predicted sizes fall in between the size frequency modes. Parameter values estimated from the fit forced through 5mm were: L_∞ = 266.3, k =0.184 and t_0 = -0.103. The lengths-at-age predicted by this curve were used for all subsequent calculations. The standard deviation of mean size-at-age was estimated by fitting a finite mixture distribution model to the length frequency data (Macdonald 2010), and converted to standard error using the sample sizes from Hauser (1969).

Fecundity was described as a function of total length (TL) by performing log-linear regression (Figure 2; $\ln(f)=1.87\cdot\ln(TL) - 1.93$; $R^2=0.70$, N=21) on data extracted using image software from the Montana Populations of Mountain Sucker (Hauser 1969, Tummers 2006). Mean fecundity for each age-class was calculated using mean size-at-age, and multiplied by the sex ratio (0.5). Uncertainty in fecundity was extrapolated from uncertainty in size-at-age (see above) by applying the delta method (variance estimation for transformed parameters; Oehlert 1992).

Size-dependent mortality was estimated by combining a size-dependent mortality model (Lorenzen 2000) with von Bertalanffy growth parameters and a catch curve analysis of the age-frequency data (Hilborn and Walters 1992). The ages of un-aged fish were calculated based on their lengths, using the fitted von Bertalanffy growth curve above. Since fish were collected throughout the summer and fall, the ages were adjusted based on sampling date to simulate a single sample. Mortality was assumed to decline proportionally with increases in size (Lorenzen 2000) such that

$$M_t = \frac{m_0}{L_t}, \quad (1)$$

where M_t and L_t are the instantaneous mortality and mean length at time t, and m_0 is the mortality at unit size (i.e., at L_t = 1). If L_t is described by the von Bertalanffy growth curve equation, survival from age j to age j+1 can be calculated by integrating equation (2) and evaluating between j and j+1:

$$s_{j\ldots j+1} = \left[\frac{L_j e^{-k}}{L_{j+1}}\right]^{m_0/kL_\infty}. \quad (2)$$

k and L_∞ are parameters of the von Bertalanffy growth equation as evaluated above. The parameter m_0 can be estimated by performing a modified catch curve analysis where logged frequencies are binned based on equation (4), so that m_0 can be described by the slope of the catch curve regression (β), scaled by the von Bertalanffy parameters (equation 5).

$$\ln L_t + kt \quad (4)$$

$$m_0 = -kL_\infty\beta \quad (5)$$

Weighted catch curve regressions were performed to decrease the bias from rarer, older fish (Freund and Littell 1991; Maceina and Bettoli 1998). Survival from stage j to stage j+1 was calculated using equation (3). Variance for each survival rate was approximated by first translating the standard error of β from the catch curve regression into a standard error for m_0, then applying the delta method (Oehlert 1992) to equation (3) to estimate the variance of the

transformed parameter. Survival and fecundity rates for stochastic simulations were drawn from lognormal distributions with mean and variances as described above. Generation time was calculated from the age-specific survival and fecundity estimates as per Caswell (2001), and yielded a generation time of 3.3 years for Mountain Sucker. Reported ages at maturity for Mountain Sucker vary from 2-5 years (Hauser 1969; Wydoski and Wydoski 2002). Mature individuals were observed in Canada as small as 65 mm (male) or 78 mm (female). Based on the modes of the length frequency histogram, we assumed that all fish are mature by age 3, and a proportion (*pr*) mature at age 2 (mean 50%, with stochastic proportions drawn uniformly from 0 – 100%). The largest fish from DU2 populations (188 mm) was estimated to be 6 years, based on the fitted growth parameter, and this was used in the model for maximum age.

Table 1. Mean and standard deviation of vital rates for Mountain Sucker. Survival probabilities are annual from age j-1 to age j. Fecundities represent annual total offspring (male and female).

Age		1	2	3	4	5	6
Length		49	85	116	141	162	180
Survival	mean	0.0036	0.184	0.328	0.418	0.478	0.520
	standard deviation	0.004	0.058	0.068	0.067	0.065	0.063
Fecundity	mean	NA	593	1048	1516	1966	2381
	standard deviation	NA	46	57	86	85	98

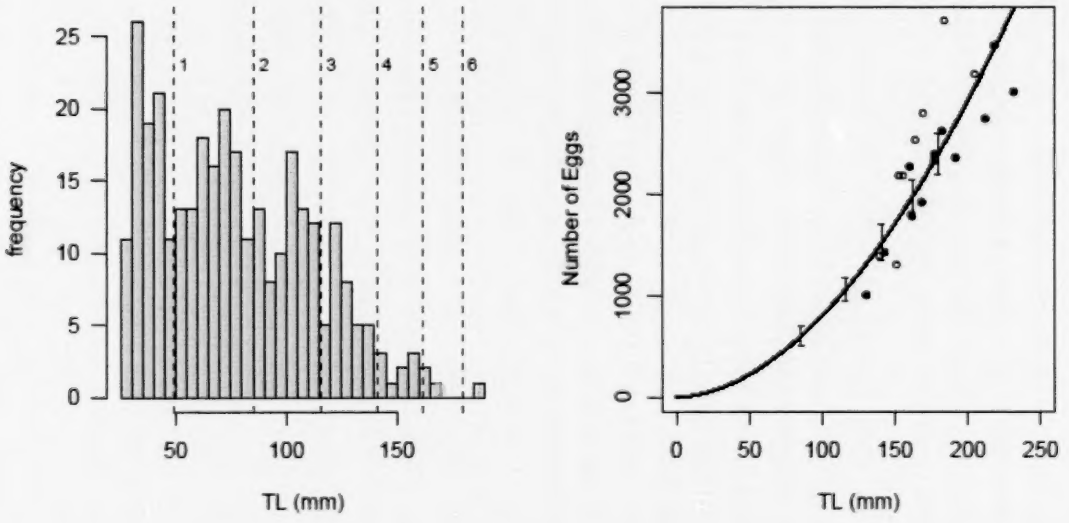


Figure 2. Length frequency of Mountain Sucker, DU2 populations, sampled between 2003 and 2009. Predicted sizes for ages 1 to 6 are overlaid, based on a Von Bertalanffy growth curve fit to mean size at age data from Hauser (1969). Right: size-specific fecundity (total number of eggs) of Mountain Sucker collected in Montana (Hauser 1969), with fitted exponential curve and 95% confidence intervals for mean fecundity-at-age overlaid.

ALLOWABLE HARM AND REQUIRED RECOVERY EFFORTS

We assessed allowable harm and minimum required recovery effort within a demographic framework following Vélez-Espino and Koops (2007; 2009a; 2009b). Briefly, we focused on

estimates of annual population growth rate (λ) as determined by the largest eigenvalue of the projection matrix (Caswell 2001). Setting equilibrium (i.e., $\lambda_{target} = 1$) as the minimum acceptable population growth rate, allowable harm (τ_v) and maximum allowable harm ($\tau_{v,max}$) were estimated analytically as:

$$\text{(6a)} \qquad \tau_v < \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right) \text{ and } \tau_{v,\max} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right)$$

where ε_v is the elasticity of vital rate *v*, and λ is population growth rate in the absence of additional harm (see below). Similarly, for populations in decline, the minimum recovery efforts (minimum increase in vital rates necessary to stabilize or stimulate population growth) were estimated as

$$\text{(6b)} \quad \psi_v > \left(\frac{1}{\varepsilon_v}\right)\left(\frac{\lambda_{target}-\lambda}{\lambda}\right) \text{ and } \psi_{v,\min} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{\lambda_{target}-\lambda}{\lambda}\right).$$

Elasticities are a measure of the sensitivity of population growth rate to perturbations in vital rate *v*, and are given by the scaled partial derivatives of λ with respect to the vital rate:

$$\text{(7)} \qquad \varepsilon_v = \frac{v}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial v}.$$

Here, a_{ij} are the matrix elements.

In addition to calculating the elasticities of vital rates deterministically, as described above, we also incorporated variation in vital rates to determine effects on population responses from demographic perturbations. Computer simulations were conducted using R (R Development Core Team 2010), with code modified from Morris and Doak (2002), to (i) generate 5000 matrices, with vital rates drawn from distributions with means and variances as described above (see Vélez-Espino and Koops 2007); (ii) calculate λ for each matrix; (iii) calculate the ε_v of G_i and f_i for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. For each vital rate, we then calculated minimum required recovery effort for the mean, maximum (upper 95% CI), and minimum (lower 95% CI) values that were based on the mean λ as calculated in these stochastic simulations.

Because human activities often impact multiple vital rates simultaneously, we also used elasticities to approximate allowable simultaneous harm or recovery efforts to survival or fertility rates. Cumulative harm or recovery efforts were estimated, respectively, as

$$\text{(8)} \qquad \mathrm{T} \approx \left(\frac{1-\lambda}{\lambda}\right)\Big/\sum_{v=1}^{n}\varepsilon_v \quad \text{or} \quad \Psi \approx \left(\frac{\lambda_{target}-\lambda}{\lambda}\right)\Big/\sum_{v=1}^{n}\varepsilon_v$$

where *n* is the number of vital rates that are simultaneously affected, ε_v is the elasticity of vital rate *v*, and T (ψ) is allowable harm (recovery effort) expressed as a single multiplier of all vital rates of interest.

RECOVERY TARGETS

We used demographic sustainability as a criterion to set recovery targets for Mountain Sucker. Demographic sustainability is related to the concept of a minimum viable population (MVP; Shaffer 1981), and was defined as the minimum adult population size that results in a desired probability of persistence (see below) over 100 years (approximately 30 generations of Mountain Sucker). We estimated MVP for individual populations, not the species in total. To estimate MVP, we assumed discrete populations that function as demographically independent units (i.e., little or no immigration or emigration). Therefore, MVP does not represent a target for the total Mountain Sucker population, but applies separately to each of the three isolated populations in DU2.

We estimated recovery targets as follows: (i) 50 000 projection matrices were generated using the means, variances, and distributions as in the allowable harm analysis, and based on a geometric mean growth rate of λ=1; (ii) projection matrices were drawn at random from these to generate 5000 realizations of population size per time step (i.e., over 100 years); (iii) these realizations were used to generate a cumulative distribution function of extinction probability, where a population was said to be extinct if it was reduced to one adult (female) individual; (iv) this process was repeated 10 times, giving an average extinction probability per time step. Catastrophic decline in population size, defined as a 50% reduction in abundance, was incorporated into these simulations, and occurred at a probability (P_k) 0.10, or 0.15 per generation (0.031 or 0.047 annually). We used these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 100 years. For these simulations, survival rates were adjusted, with constant variance, by optimizing m_0 so that the population growth rate was at equilibrium (geometric mean of λ=1). This was done to simulate the probability of persistence of a stable population over the long term, since population growth is not sustainable over time.

MINIMUM AREA FOR POPULATION VIABILITY

Following Vélez-Espino *et al.* (2010), we estimated the minimum area for population viability (MAPV) as a first order quantification of the amount of habitat required to support a viable population. We calculated MAPV for each age-class in the population as:

$$(9) \quad MAPV_j = MVP_j \cdot API_j.$$

MVP_j is the minimum number of individuals per age-class required to achieve the desired probability of persistence over 100 years, as estimated for the recovery target. Individuals were distributed among age classes according to the stable age distribution, which is represented by the dominant right eigenvector (w) of the mean projection matrix ($\mathbf{M}\, w = \lambda \cdot w$) (De Kroon *et al.* 1986). The recovery target, MVP, is expressed in terms of adult numbers only (ages 2-6). API_j is the age-specific area required per individual (the inverse of density). We estimate API based on an allometry for freshwater fishes in river environments from Randall *et al.* (1995):

$$(10) \quad API = e^{-13.28} \cdot TL^{2.904}$$

where TL is the average total length in mm.

The API for each age class was estimated from equation (10) in two ways: (i) using the geometric mean of lengths at the endpoints of each class as predicted by the fitted von Bertalanffy growth curve, or (ii) estimating young-of-the-year (YOY) and juvenile API as before, but adult API as the inverse of the density of Mountain Sucker found in California (248 fish per

hectare; Moyle and Vondracek 1985). An MAPV for each stage was estimated from equation (9), and the MAPV for the entire population was estimated by summing across all age classes.

RECOVERY STRATEGIES AND TIMES

The effects of three hypothetical recovery strategies are compared. Since it is likely not possible to direct efforts toward individual vital rates, we focused on positive changes in annual survival probability in early life (i.e., $s_{1,2}$), in adults ($s_{3..6}$), or in fertility ($f_{2..6}$) that might result from specific recovery actions (e.g., the rehabilitation or enhancement of habitat). Specifically, each strategy consisted of improving the associated vital rates by either 10% or 20% to demonstrate the relative performance of investing in different recovery actions. We also explored maximum plausible improvements to each rate, which we defined as the proportion improvement required for the mean values of each rate to reach the upper 95% confidence bound.

Recovery was simulated in a similar manner to the recovery targets. Projection matrices were drawn to determine status quo dynamics (i.e., in the absence of harm or recovery), and for each strategy the means of the associated vital rates were increased by the appropriate increment before randomly generating projection matrices. We then used 3 000 realizations of population size over 250 years to generate a median time to extinction. Results were averaged over 5 runs. The probability of extinction (or recovery) at time t was equal to the proportion of realizations of population size that fell below the extinction threshold (or reached the recovery target) at time t. The recovery target was set at MVP, and time to recovery was defined as the time at which 95% of simulations had reached the recovery target.

RESULTS

MINIMUM RECOVERY EFFORTS

Based on the ranges of vital rates of the Mountain Sucker as described above, we estimate that populations are, on average, in decline ($\lambda = 0.78$). However, the 95% confidence interval around this estimate, based on stochastic simulations, includes equilibrium and also fairly significant growth (0.5 – 1.3). Given the uncertainty around these estimates, the trajectory of Mountain Sucker cannot be confirmed as either increasing or decreasing.

It is likely impossible to isolate harm or recovery to individual age classes, but the additive nature of elasticities allows us to consider the collective effects of perturbations on different life stages. When rates affecting juvenile or adult life stages were considered cumulatively, elasticity analysis showed that the population growth rate is very sensitive both to perturbations of adult survival ($s_{3..6}$) and to survival of YOY and juveniles (Figure 3). Although the means of deterministically and stochastically determined elasticities are nearly identical, elasticities are still sensitive to stochastic variation (Figure 3, panel 2). Comparing correlations among vital rates and elasticities shows that the uncertainty in these elasticities can be largely attributed to uncertainty in the estimate of age-0 survival; higher juvenile survival decreases the influence of both adult survival and fecundity of the oldest fish. Uncertainty about the proportion of reproducing age 2 individuals (p_r) also drives elasticity uncertainty; higher proportions result in a lower elasticity for survival to age 3. Variation in age-0 survival also explains 86% of the variation in the population growth rate. The pattern of elasticities is also sensitive to whether the population is growing or in decline. When there is population growth, the population is very sensitive to changes in juvenile survival. Declining populations, however are more sensitive to changes in adult survival and reproduction, and the importance of fecundity increases with age.

The minimum recovery efforts for each vital rate depended on the stochastic element (e.g., mean or upper or lower 95% CI; Table 2). Two target growth rates are compared: i) the

proportional improvements required to achieve stabilization ($\lambda = 1$), and ii) the improvements required to achieve the inverse of the rate of decline, or $\lambda = 1.28$). From a precautionary perspective (i.e., assuming the highest effort of all methods), our results suggest that a minimum improvement of 78% to juvenile survival (both ages 0 and 1), 114% to survival of adults, or 46% to survival of all ages is required to reach stabilization. A fecundity rate that is 344% higher than the current estimate would be required for the same result. When choosing a recovery strategy, the scope for improvement should also be considered. Table 2 presents the absolute maximum scope for improvement (i.e., supposing survival could potentially be 100%, and no bounds for fecundity), and a plausible scope for improvement. The plausible scope compares the mean survival rates with the upper 95% confidence bound as generated in stochastic simulations. While the target growth rate of 1.28 is attainable based on the maximum scope, it is not within the plausible scope. Table 2 also shows the mean expected growth rate if the plausible scope for improvement is achieved. Population growth is plausible ($\lambda = 1.09$) given sufficient improvements in juvenile survival (84%). If recovery efforts do not meet at least one of these thresholds, the future survival and recovery of individual populations may be compromised.

The minimum recovery efforts required are very sensitive to the assumed population growth rate of 0.78. If new evidence suggests that the growth rate was underestimated, the required recovery efforts could decrease considerably. For instance, a sampling bias that results in an under-representation of the largest individuals will cause mortality to be over-estimated.

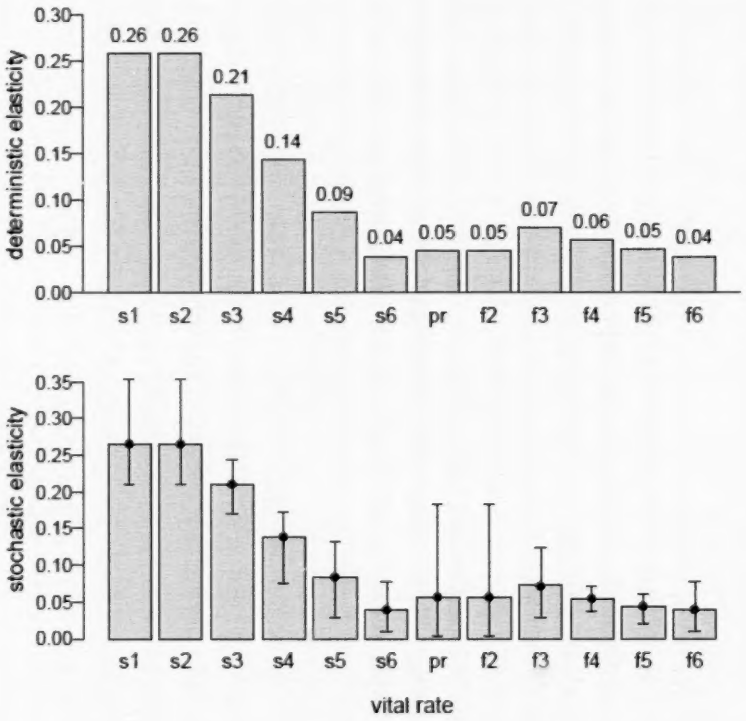


Figure 3. Results of the deterministic (panel 1) and stochastic (panel 2) perturbation analysis showing elasticities (ε_v) of the vital rates: annual survival probability of age j-1 to age j (s_j), fertility (f_j), and the proportion of reproductive age 2 individuals (pr). Exact values are shown above bars. Stochastic results include associated bootstrapped 95% confidence interval.

*Table 2. Summary of minimum recovery effort ($\psi_{v,min}$) estimates for combined vital rates of Mountain Sucker, based on a stochastic perturbation analysis and a population growth rate (λ) of 0.78, and a target growth rate (λ_{target}) of 1 (stabilize population) or 1.28 (stimulate growth). s_j = juvenile survival (age 0 to maturity); s_a = adult survival (maturity to age 6); s_n = survival of all ages; f = fecundity, All = all survival and fecundity rates. Max. scope = maximum proportion improvement (100% survival). Plausible scope = proportion improvement required for mean to reach the upper 95% confidence interval from stochastic simulations. Plausible growth = geometric mean population growth rate assuming a vital rate increase equal to the plausible scope. *Estimates are independent of growth target*

	target =1					target=1.28				
	s_j	s_a	s_n	f	All	s_j	s_a	s_n	f	All
Deterministic	0.65	0.70	0.34	1.30	0.26	1.37	1.47	0.71	2.74	0.54
Stochastic	0.63	0.69	0.33	1.25	0.25	1.34	1.46	0.70	2.68	0.53
+ 95% CI	0.46	0.53	0.25	0.66	0.16	0.98	1.13	0.53	1.42	0.35
- 95% CI	**0.78**	**1.14**	**0.46**	**3.44**	**0.41**	**1.66**	**2.43**	**0.99**	**7.34**	**0.87**
Max. Scope*	4.43	0.92	0.92	NA	0.92	4.43	0.92	0.92	NA	0.92
Plausible scope*	0.84	0.28	0.28	0.04	0.28/0.04	0.84	0.28	0.28	0.04	0.28/0.04
Plausible growth (λ)*	1.09	0.86	0.98	0.78	0.99	1.09	0.86	0.98	0.78	0.99

RECOVERY TARGETS

Probability of extinction decreases as a power function of population size (Figure 4). Functions of the form $y = a \cdot x^{-b}$ were fitted, using least squares and the logged values of x (population size) and y (extinction probability), to the simulated extinction probabilities for each catastrophe scenario.

While choosing a larger recovery target will result in a lower risk of extinction, there are also costs associated with an increased target (increased effort, time, etc.). When determining MVP from the fitted power curves, we attempted to balance the benefit of reduced extinction risk and the cost of increased recovery effort with the following algorithm. (i) We assumed that the maximum allowable risk of extinction is 10% based on COSEWIC's quantitative criteria (E) that a risk of extinction greater than or equal to 10% within 100 years constitutes Threatened status. We define a maximum MVP (i.e., maximum feasible effort) to be the population that would result in a 0.1% probability of extinction, as this is the most stringent criteria in the literature; (ii) using these as boundaries, we calculate the average decrease in probability of extinction per individual increase in population size; (iii) we choose as MVP the population size that would result in this average (i.e., the point on the power curve at which the slope equals the average % decrease in extinction risk per increase in target). This represents the point between the upper and lower boundaries where the reduction in extinction risk per investment in recovery is maximized. Calculated in this way, MVP was 260 adults aged 2-6 when the probability of catastrophic decline (50%) was assumed to be 10% per generation (3.1% annually). If catastrophes occurred at 15% per generation (4.7% annually), MVP was 570 adults. In both scenarios, the probability of extinction for the respective MVPs was approximately 0.01 over 100 years (Figure 4). The extinction risk, P(ext.), for the 15% per generation catastrophe scenario can be defined as a function of initial adult population, N, as:

$$(12a) \quad P(ext.) = 13 \cdot N^{-1.10}.$$

MVP simulations assumed an extinction threshold of 1 adult female (or 2 adults). We observed that assuming a higher, quasi-extinction threshold (i.e., if the population is considered effectively extinct before it declines to 1 female) results in a roughly linear increase in MVP. For

example, if the quasi-extinction threshold is defined as 50 adults, and the chance of catastrophe is 15% per generation, mean MVP increases from 570 to 6400 (range over 10 trials: 4600 – 8400) adults (Table 5), and the extinction risk as a function of adult population size is:

(12b) $P(ext.) = 84 \cdot N^{-1.03}$.

Thus, if the true extinction threshold is greater than 1 adult female, larger recovery targets should be considered. The relationship between MVP and the extinction threshold (ET; number of adults), for a catastrophe probability of 15% per generation, can be approximated for any values of ET as

(13) MVP = 118·ET + 447.

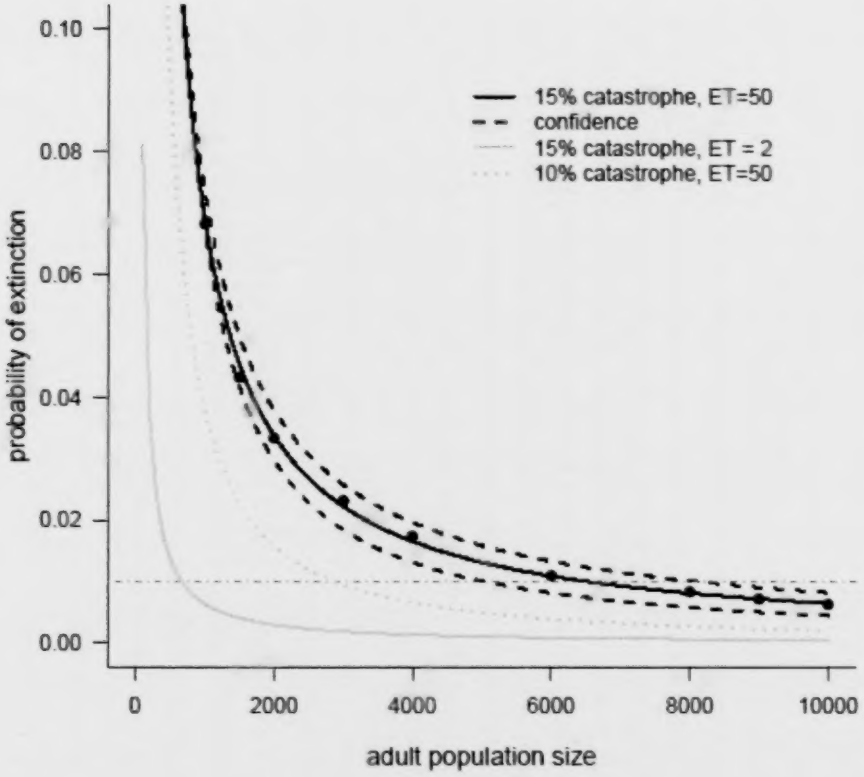


Figure 4. Probability of extinction within 100 years of 10 simulated Mountain Sucker populations, at equilibrium, as a function of adult population size. Black curves assume a 15% probability of catastrophic decline (solid = mean, dotted = max and min of 10 runs), and an extinction threshold of 50 adults. Grey curves represent 10% probability of catastrophe (dotted), or 15% probability of catastrophe and an extinction threshold of 2 adults. Dashed horizontal reference line is at 0.01 and intersects curves at the associated MVPs (Table 5).

RECOVERY TIMES

Under current estimated conditions (i.e., assuming a population growth rate of 0.78), and in the absence of recovery efforts or additional harm, a population of 6400 (MVP) was predicted to go extinct in 32 years (range: 19 – 55 years; Figure 5). Improving the survival of juveniles or of adults by 20% delayed this extinction time to 51 or 55 years respectively (Table 3). When survival of all ages was improved by 28% (the plausible scope for change), the population nearly stabilized, and the risk of imminent extinction was eliminated. The scope for improvement to fecundity was small, and did not result in a decrease in extinction risk. Population growth (λ = 1.08) was achieved by improving juvenile survival by 84% (the plausible scope for improvement). At this rate, a population at 10% of MVP (640 adults) was predicted to have a 95% chance of recovering (reaching MVP = 6400 adults) within 43 years. If adult survival was additionally improved by 28%, the resulting growth rate (λ = 1.20) reduced the recovery time to 21 years.

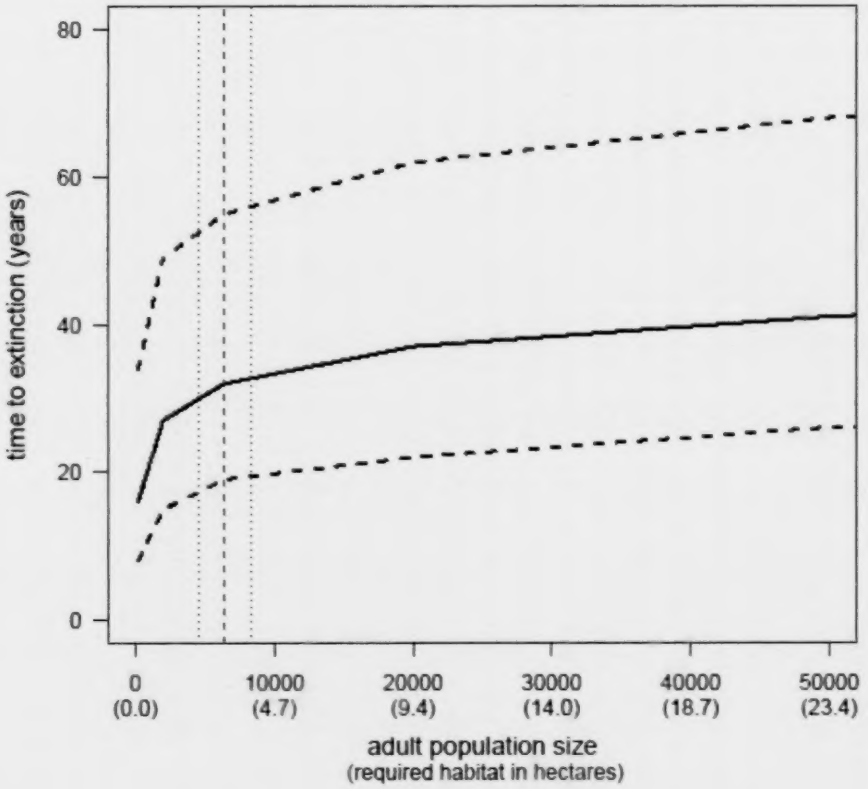


Figure 5. Time to extinction of 10 simulated Mountain Sucker populations in decline (λ = 0.78), as a function of adult population size. Median (solid) and 95% bootstrapped confidence interval (dashed). Vertical reference lines represent the Minimum Viable Population size (MVP = 6400 adults) and stochastic confidence interval. Minimum Area for Population Viability (MAPV), in hectares, for each population size is also shown (brackets).

*Table 3. Effects of recovery efforts on: expected (median) time to extinction, mean stochastic rate of population growth/decline, and the risk of extinction within 100 years of a Mountain Sucker population at MVP. If a strategy resulted in growth, the expected time to 95% probability of recovery (starting from 10% of MVP) is shown. Recovery strategies are s_j = juvenile survival (hatch to age 2), s_a = adult survival, and s_n = survival of all ages. Best strategies (most likely to result in stabilization or growth) are highlighted. *Represents a 28% and an 84% increase in adult and juvenile survivals, respectively.*

	Strategy									
	s_j			s_a			s_n			
Effort	10%	20%	84%	10%	20%	28%	10%	20%	28%	28/84%*
Time to extinction	40	51	>250	41	55	67	55	163	>250	>250
Growth rate (λ)	0.80	0.81	**1.09**	0.80	0.83	0.86	0.84	0.92	**0.98**	**1.20**
Extinction risk (100 years)	1.00	0.97	**0.00**	1.00	0.94	0.84	0.95	0.23	**0.01**	**0.00**
Recovery Time	NA	NA	**43**	NA	NA	NA	NA	NA	**NA**	**21**

MINIMUM AREA FOR POPULATION VIABILITY

The stable stage distribution for Mountain Sucker is 99.04% YOY, 0.69% age 1, and 0.27% adult individuals (ages 2-6; Table 4). With a target MVP of 6400 adults, under a 0.15 probability of catastrophe per generation and assuming an extinction threshold of 50 adults, a population of this size was predicted to require 3.0 ha of suitable habitat (MAPV) or 16.6 ha ($MAPV_2$; Table 5). This area assumes that each individual requires the areas listed in Table 4, and does not account for any overlapping of individual habitats (sharing) that may occur. It also assumes that habitat is of suitable quality, and should be increased if the quality of habitat is low.

Table 4. Stable stage distribution (SSD, percentage of the population in each stage), and area per individual (method (i): API allometry (eqn 10); method (ii): API_2 observed adult density in California) by stage.

SSD (%)	API (m^2)	API_2 (m^2)
99.04	0.005	0.005
0.69	0.31	0.31
0.27	1.08 - 6.74	23.36

Table 5. Number of individuals for each age class to support a minimum viable population (MVP) and the resulting estimate of required habitat for each stage and for the entire population, based on (i) geometric mean size of stage (MAPV), or (ii) observed density of Mountain Sucker in California ($MAPV_2$). Results for three different extinction thresholds and two probabilities of catastrophe are shown.

		Catastrophe = 10%			Catastrophe = 15%		
Extinction threshold	Age class(es)	MVP	MAPV(m^2)	$MAPV_2$(m^2)	MVP	MAPV (m^2)	$MAPV_2$(m^2)
2	0	96783	485	484	211 433	1 061	1 057
	1	679	210	210	1 483	458	460
	2-6	**260**	520	6 074	**568**	1 135	13 268
	Total		**1 215**	**6 768**		**2 654**	**14 785**
20	0	420632	2 110	2 103	1 027 384	5 153	5 137
	1	2950	911	915	7 204	2 225	2 233
	2-6	**1130**	2 262	26 397	**2 760**	5 525	64 474
	Total		**5 283**	**29 414**		**12 903**	**71 844**
50	0	950702	4 769	4 754	2 380 851	11 942	11 904
	1	6666	2 060	2 066	16 695	5 158	5 175
	2-6	**2554**	5 118	59 661	**6 396**	12 803	149 411
	Total		**11 947**	**66 481**		**29 903**	**166 490**

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Mountain Sucker, human-induced harm to the overall survival of all life stages should be minimal. Current estimates suggest that DU2 populations may be in decline. Recovery efforts that alleviate current harms or improve current conditions are recommended. For example, stabilization of the population (target growth rate of $\lambda = 1$) could require as much as 78% improvement in juvenile survival, or 46% improvement in survival of all ages (Table 2). The required improvement to adult survival (114%) was not within the scope of improvement for a survival rate. These efforts will be sufficient when abundance exceeds the Minimum Viable Population (MVP) recovery targets described below. For populations that do not exceed MVP, we recommend minimum target improvements that result in mean population growth. Simulations showed that an 84% improvement to juvenile survival and a 28% improvement to adult survival are expected to result in mean population growth of $\lambda = 1.2$ (Table 3). These levels represent the maximum plausible increases, based on parameter confidence intervals. It is important to note that estimates of recovery efforts assume that the population growth rate before harm (λ) is 0.78. If research indicates that any of our parameters are underestimated, required recovery efforts will be reduced; stability or growth of DU2 populations is within the confidence interval for the estimated population growth rate.

In addition to providing estimates of recovery efforts, this work also provides recovery targets based on the concept of MVP. The MVP was estimated at 570 adults when the probability of a catastrophic (50%) decline (P_k) was 0.15 per generation and an extinction threshold of 2 adults. Increasing the extinction threshold to 50 adults results in an MVP of 6400 adults. A threshold of 50 adults is recommended in the literature for maintenance of genetic diversity (Simberloff 1988). According to Reed *et al.* (2003), catastrophic events (a one-time decline in abundance of 50% or more) occur at a probability of 0.14 per generation in vertebrates. We therefore recommend recovery targets based on a 15% probability of catastrophe, but suggest that data be collected to confirm the frequency and severity of catastrophic decline experienced by Mountain Sucker. Recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation or allowable harm. A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery. We stress that these MVP targets refer to adult numbers only. If juveniles are being included in abundance estimates, then the MVP should include these age classes as well (see Table 5).

Our analyses show that with the currently estimated rate of population decline ($\lambda = 0.8$), in the absence of recovery efforts or additional harm, and assuming a 15% probability of catastrophic decline, a population at MVP will be extirpated in 32 years. The current population size is unknown, however, and a time specific to DU2 cannot be estimated. Regardless, to delay time to extirpation, we recommend recovery actions that increase the annual survival rate of Mountain Sucker in excess of 25% and as much as 46% to significantly reduce the extinction risk. Efforts to improve fecundity by a similar proportion are expected to be much less effective.

Our analyses of recovery targets (MVP) predict that populations will have a low probability of extinction with 6400 adults (Figure 4). However, our projections of recovery times predict that populations of these sizes have a median time to extinction of 19 – 55 years (Figure 5). The reason for these seemingly disparate results is the difference in population growth rates for these two analyses. When identifying a recovery target, we assumed that population growth had been stabilized and the population was at equilibrium ($\lambda = 1$), whereas time to extinction

was projected with the current population growth rate ($\lambda = 0.78$). This emphasises the importance of determining the drivers of population decline and stabilizing population abundances.

Model results suggest that a recovered population of Mountain Sucker requires 0.3 – 1.5 ha of suitable habitat if the extinction threshold is 2 adults, or 3.0 – 16.6 ha if the extinction threshold is 50 adults. Isolated groups having insufficient quality or quantity of habitat may be at an exponentially increased risk of extirpation due to density dependence (Young and Koops 2010, 2011).

True MAPV likely falls within the estimated range. The lower bound, which was based on a size allometry, is likely too small; targeted sampling in South Dakota, at sites where Mountain Sucker were known to occur, produced a mean density of 1262 fish/ha, and site specific densities as high as 8344 fish/ha (Dauwalter *et al.* 2008). An MAPV of 3 ha containing 6400 adults would imply a target density of 2133 fish/ha. The required density has therefore been observed, but only in ideal habitat. An MAPV of 3 ha may be too optimistic unless the rivers of DU2 are ideally suited for Mountain Sucker throughout. In addition, the allometry was based on temporally fixed density estimates, and does not account for seasonal movement of the species. If Mountain Sucker swim upstream to spawn, for instance, then total MAPV would include 3 ha of overwintering habitat plus spawning habitat, as well as all corridors necessary for movement between the areas. The upper bound of the MAPV range, which was based on a density estimate of 428 fish/ha, is likely too conservative given that Mountain Sucker have been observed to persist at much higher densities. It should be cautioned that neither bound reflects site-specific data pertaining to the DU2. Further study of site-specific densities, as well as movement and subsequent space requirements of Mountain Sucker would aid in the refinement of habitat targets.

We do not have any data to estimate abundance of Mountain Sucker in any of the three populations in DU2, and therefore cannot determine whether these populations exceed the MVP target of 6400 adults or not. However, consensus among experts at the Mountain Sucker RPA meeting (DFO 2013) was that the Milk rivers population likely exceeds this target, but that the Battle Creek and Frenchman River populations do not. These opinions were based on a comparison of qualitative observations of Mountain Sucker densities, against the densities that would be implied by 6400 or more adults in each of the available habitats. The Milk rivers population has available approximately 12 ha of potential habitat, including the North Milk River and the Milk River downstream of its confluence (DFO, unpubl. data). The density of Mountain Sucker in this system was thought to surpass the implied required density of $0.5/m^2$ adult Mountain Sucker. We stress that without evidence of population growth or stability, achieving the MVP target is not sufficient to guarantee a "recovered" status of the population. Harm to the overall survival of this population should not be allowed if it is in decline. Further study is needed to confirm or correct the estimated downward trajectory.

Battle Creek and the Frenchman River are much smaller than the Milk rivers. Densities in these systems are not thought to be sufficient to achieve MVP, and it was proposed at the Mountain Sucker RPA meeting that population abundances may never have exceeded the recommended target (DFO 2013). Since a target of 6400 adults may not be feasible for the Saskatchewan populations, they will be subject to a higher risk of extinction (Figure 4, Equation 12b). Threats to Mountain Sucker will likely have a greater impact on Battle Creek and Frenchman River populations than the same threats in the Milk rivers, and should be managed with this in mind.

UNCERTAINTIES

We emphasize the need for research on Mountain Sucker in Canada, and in DU2 in particular, to determine (i) survival rates during early life, (ii) the accuracy of our adult survival estimates, (iii) population abundance or density and its trajectory, (iv) movement patterns of Mountain Sucker, and (v) the frequency and extent of catastrophic events for these populations.

In lieu of direct estimates of survival of immature individuals our analysis assumed that a size-dependent mortality schedule was representative. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. Uncertainty in age-0 survival had a relatively large impact on both the population growth rate and elasticity values, and consequently strongly influenced recommendations. The range of population growth rates achieved in stochastic simulations was very wide (0.5-1.3) and included $\lambda = 1$. Therefore, if the true mean values of some (or all) vital rates are in the higher ranges of their confidence intervals, then populations could be experiencing a higher growth rate than the estimated mean above, and may not be in decline. More accurate estimates of uncertain vital rates are needed to confirm the status of Mountain Sucker populations. In lieu of early-life survival estimates, we stress the importance of determining the true population growth rate.

Our recommended habitat target was very uncertain due to a lack of information about the density at which Mountain Sucker can persist, as well as any additional space they may require for seasonal movement. The choice of recovery target is also impeded by a lack of information regarding catastrophic events; targets and model predictions vary widely depending on the frequency of catastrophic decline in the population. Research that addresses these issues will greatly reduce the uncertainty in estimates of both abundance and habitat targets, and thus in recommendations for the conservation of Mountain Sucker in Canada.

Finally, predictions from this model assume random mating and complete mixing of the population (i.e., all individuals interact and can reproduce with one another). This assumption should be considered when applying MVP targets, and larger total targets should be set if the assumption does not hold.

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